

REALIGNMENTS IN THE DICHANTHELIUM  
ACUMINATUM COMPLEX (POACEAE)

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When Gould and Clark (1978) placed 46 names in synonymy under Dichantherium acuminatum (Sw.) Gould & Clark a cycle of "lumping - splitting - lumping" spanning a century was nearly completed. Their broad circumscription of this taxon approached the view held as late as the sixth edition of Gray's Manual (Watson and Coulter, 1889) which treated this complex and more as a single species, Panicum dichotomum L. In the two decades following this edition 36 new species were named in the complex, most of them by Nash (1896, 1897, 1898, and 1903) and Ashe (1898 and 1900). Hitchcock and Chase (1910) recognized 24 species for this group in their revision of North American Panicum. Although six new species were named in the next four decades, the trend toward reduction in the number of recognized species is evident in the works of Deam (1929), Fernald (1921, 1934, and 1950), Shinnars (1944), Pohl (1947), Gleason (1952), Steyermark (1963), Radford et al (1964), and Lelong (1965).

This exceptional range of taxonomic treatments can be attributed to the problems created for the taxonomist by the reproductive biology of these grasses. Reproduction is amphigamous (sensu Hackel as reviewed by Uphoff, 1938) with autogamy predominating (Lelong, 1965; Spellenberg, 1975a). The autogamous reproduction produces innumerable essentially homozygous local populations or microspecies, some of which have incorporated translocations or inversions relative to other populations. An exceptional range of variation in such traits as habit, pubescence, and spikelet length is maintained in the complex probably through inbreeding. Sporadic outcrossing introduces new traits into inbred populations leading to new homozygous lines. Spellenberg (1968, 1970, 1975b) synthesized an array of hybrids between populations and between recognized species. He noted that the fertility of the hybrids was generally low and that it tended to be lowest in hybrids between plants widely separated geographically or morphologically, but that successive generations of hybrid derivatives showed increasing fertility. These observations reinforce the views of some workers in this group that natural hybridization is sufficiently extensive to blur distinctions between species or microspecies and to produce a reticulum of intergrading forms between described taxa. Environmentally induced alterations of many of the diagnostic traits further obscure distinctions between taxa.

A satisfactory taxonomic treatment, if such is possible in a large amphigamous complex, will require extensive work with synthetic hybridization, population studies, and transplant garden or growth chamber observations. Lelong's study on variation and Spellenberg's work with artificial hybridization are major contributions, but are limited to portions of the complex. Thus the taxonomy of the D. acuminatum complex still rests to a large extent on the study of herbarium specimens and on personal judgment.

Until recently the D. acuminatum complex was called the Panicum lanuginosum complex. A range of treatments and combinations were available to the taxonomist based on the assumptions that the group belonged in the genus Panicum and that P. lanuginosum was the oldest valid binomial in the complex. In 1974 Gould raised the subgenus Dichantherium of Panicum to a genus, supported by the work of Hsu (1965), Clark and Gould (1975), and Brown and Smith (1975). In 1978 Gould and Clark, noting that P. acuminatum predated P. lanuginosum, published D. acuminatum as a new combination and assigned most of the P. lanuginosum complex to varieties of this species. Since I believe that their treatment overlooks some of Spellenberg's and Lelong's work and fails to recognize certain species and varieties which I and many previous workers consider to be worthy of recognition I am compelled to make several modifications to their work.

#### Key to the species:

1. Peduncle, panicle axis, and sheaths of primary (vernal) culm puberulent with hairs about 0.1 mm long, sometimes also pubescent with longer hairs, but never grayish-villous.
2. Spikelets 0.8-1.1 mm long; blades usually less than 4 mm wide and 4 cm long; sheaths sparsely puberulent, lacking papillose-based longer hairs..... D. wrightianum
2. Spikelets 1.2-1.7 mm long; mid-culm blades more than 4 mm wide and 4 cm long; sheaths with some papillose-based hairs 2 mm long or more.
3. Mid-culm blades nearly erect, glabrous above, generally 4-7 mm wide and 4-7 cm long; sheaths sparsely pilose with hairs 1-2 mm long; ligule of hairs 1-2.5 mm long intermixed; spikelets 1.2-1.4 mm long..... D. leucothrix
3. Mid-culm blades ascending-spreading, pilose above, generally 3-5 mm wide and 3-5 cm long; sheaths pilose with hairs 2-4 mm long; ligule a ring of hairs approximately 0.7 mm long differentiated from the pseudoligule of scattered hairs 3-4 mm long; spikelets 1.3-1.7 mm long..... D. meridionale
1. Peduncle, panicle axis, and sheaths of primary (vernal) culm glabrous, or pilose, or grayish-villous with some shorter hairs 0.2-0.5 mm long, but not puberulent.
4. Ligule of hairs 1-2.5 mm long; sheaths glabrous; blades firm, the lower nearly erect.

5. Panicle dense and narrow, about one-fourth as wide as long, bearing 250 or more spikelets, the majority of these on pedicels less than 1.5 mm long; spikelets 1.4-1.6 mm long; fertile floret pointed, sharply acute at apex..... D. spretum
5. Panicle more open, more than one-half as wide as long, bearing about 100-150 spikelets, these mostly on pedicels 2-5 mm long; spikelets 1.2-1.5 mm long; fertile floret rounded to acute, not pointed at apex..... D. longiligulatum
4. Ligule with some hairs 3-5 mm long; sheaths pilose, villous, or nearly glabrous; blades not especially firm, the lower usually spreading-ascending.
6. Sheaths and culms with straight horizontal to retrorse hairs, the longer ones exceeding 4 mm; hairs 0.2-1 mm long absent; spikelets 1.8-2.5 mm long..... D. villosissimum
6. Sheaths and culms glabrous, or ascending pilose to hispid, or grayish-villous with a dense tangled mixture of slender hairs, a few approaching 4 mm, but usually with short hairs 0.2-1 mm long; spikelets 1.2-2.0 mm long..... D. acuminatum

Dichantheium wrightianum (Scribner) Freckmann, comb. nov.

Basionym: Panicum wrightianum Scribner, U. S. D. A. Div. Agrost. Bull. 11: 44. 1898.

Synonyms include D. acuminatum (Sw.) Gould & Clark var. wrightianum (Scribn.) Gould & Clark.

This species seems to be as closely related to some members of the Hitchcock and Chase group "Ensifolia" as to D. acuminatum from which it differs by its small, delicate culms, puberulence, relatively short ligule, and tiny spikelets.

Sandy peat or muck. Coastal Plain, Cuba, and Belize.

Dichantheium leucothrix (Nash) Freckmann, comb. nov.

Basionym: Panicum leucothrix Nash, Bull. Torrey Bot. Club 24: 41. 1897.

Gould and Clark placed this name in synonymy under D. acuminatum var. implicatum (Scribn.) Gould & Clark. It can be distinguished from D. acuminatum by its puberulent sheaths and shorter ligule hairs (longest hairs 2.5 mm vs. longest hairs more than 3 mm long).

Wet sand, muck, or peat. Coastal Plain, Cuba, West Indies, and northern South America.

Dichantherium meridionale (Ashe) Freckm. *Phytologia* 39: 270. 1978.

Synonyms include P. albemarlense Ashe.

Goald and Clark placed this name in synonymy under D. acuminatum var. implicatum. This species differs from that taxon by puberulent peduncles, panicle axes, and sheaths; by greatly reduced uppermost blades (less than 4 mm wide and 4 cm long); and generally by its exceptionally slender culms. The ligule consists of a tight ring of hairs about 0.7 mm long with scattered hairs 3-4 mm long slightly distal to it and forming an apparent pseudoligule in contrast to the ligule or pseudoligule of D. acuminatum which is composed of a dense mixture of hairs of varying length, the longest more than 3 mm but not separated from the shorter hairs. It should be noted that secondary (autumnal) shoots of D. acuminatum generally produce short hairs about 0.2 mm long among the longer hairs and are frequently mistaken for D. meridionale. These shorter hairs are slightly longer than the puberulence of D. meridionale, but accurate identification requires an examination of the remaining parts of the primary shoots for the presence or absence of puberulence.

Sand and sandy shores. Eastern United States, most common on the Atlantic coastal plain and inland through the Great Lakes.

Dichantherium spretum (Schultes) Freckmann, comb. nov.

Basionym: Panicum spretum Schultes, *Mant.* 2: 248. 1824.

Synonyms include D. acuminatum var. densiflorum (Rand & Redfield) Goald & Clark.

This species is readily distinguished from the others in the complex by the combination of glabrous peduncles, panicle axes, and sheaths together with the narrow panicles of numerous spikelets on short pedicels, and the sharply-pointed fertile florets. It has shorter ligules and firmer, more strongly ascending lower leaves than D. acuminatum var. lindheimeri (Nash) Goald & Clark.

Peat and wet sand. Coastal Plain and at scattered locations inland to Indiana.

Dichantherium longiligulatum (Nash) Freckmann, comb. nov.

Basionym: Panicum longiligulatum Nash, *Bull. Torrey Bot. Club* 26: 574. 1899.

Synonym: D. acuminatum var. longiligulatum (Nash) Goald & Clark.

This species can be confused with *D. spretum*, sparsely hairy *D. leucothrix*, and *D. acuminatum* var. *lindheimeri*. It differs from *D. spretum* by its wider, more open panicles with fewer spikelets on longer pedicels, and by the less acute fertile florets; from *D. leucothrix* by completely glabrous sheaths; and from *D. acuminatum* var. *lindheimeri* by shorter spikelets (usually less than 1.4 mm long vs. usually more than 1.4 mm), firmer, more strongly ascending lower leaves, shorter ligules, and often taller culms (usually more than 80 cm tall vs. usually less than 80 cm) with internodes more than twice as long as the sheaths.

Swamps and pine barrens. Coastal Plain and Central America.

*Dichantherium villosissimum* (Nash) Freckm. *Phytologia* 39: 270. 1978.

Synonyms include *D. acuminatum* var. *villosum* (A. Gray) Gould & Clark.

Gould and Clark placed *P. pseudopubescens* Nash in synonymy under *D. acuminatum* var. *villosum*. Fernald (1950) and Gleason treated it as a variety of *P. villosissimum* Nash. It differs by its stiff, ascending hairs on culm and sheath instead of slender spreading hairs. The poorly known *P. benneri* Fern. may be another form of *P. pseudopubescens*. I withhold judgment on both pending further study. Fernald and Gleason treated *P. scoparioides* Ashe as a variety of *P. villosissimum*. I agree with Lelong and others that it probably consists of a group of nearly sterile hybrids between *D. oligosanthos* (Schult.) Gould and *D. acuminatum*. Gould and Clark placed *P. euchlamydeum* Shinnery in synonymy under *D. acuminatum* var. *villosum* and also under *D. sabulorum* (Lam.) Gould & Clark var. *patulum* (Scribn. & Merr.) Gould & Clark. It does not seem to be closely related to the former because its sheath and culm vestiture consists of stiff, ascending hairs along with puberulence and its spikelets and very stiff panicle branches are dark red.

Key to the varieties of *D. villosissimum*:

1. Spikelets 2.1-2.5 mm long; panicle 5-10 cm long with fairly stiff branches; largest blades generally more than 6 mm wide..... var. *villosissimum*
1. Spikelets 1.8-2.1 mm long; panicle 4-6 cm long with flexuous branches; blades generally less than 6 mm wide..... var. *praecocius*

*Dichantherium villosissimum* (Nash) Freckm. var. *villosissimum*

This variety is similar to *D. acuminatum* var. *acuminatum* with some intergradation occurring. The great majority of specimens can be separated by the following key:

1. Spikelets 2.1-2.5 mm long; first glume 0.7-1.1 mm long, about one-third as long as the spikelet; longest hairs on sheaths and culms 4-5 mm long, relatively straight, horizontally spreading to somewhat retrorse; sheaths lacking hairs less than 1 mm long; panicles two to three times compound, the major branches rebranching once or twice.....  
..... D. villosissimum var. villosissimum
1. Spikelets 1.2-2.0 mm long; first glume 0.3-0.8 mm long, about one-fourth as long as the spikelet; longest hairs on sheaths and culms 3 or sometimes 4 mm long, curved or wavy, variously ascending to reflexed, somewhat tangled to matted, very dense and giving grayish color to sheath; sheath usually with shorter hairs, 0.2-1 mm long also present; panicle frequently four or more times compound, the longer branches rebranching three times.....  
..... D. acuminatum var. acuminatum

Sandy soil and open woodlands. Massachusetts to Florida and Texas; Mexico; Central America.

Dichantherium villosissimum var. praecocius (Hitchc. & Chase) Freckm. *Phytologia* 39: 270. 1978.

This variety intergrades with var. villosissimum in eastern Texas, Oklahoma, northern Arkansas, and southern Missouri. A few specimens in the northern part of its range suggest limited intergradation with D. acuminatum var. fasciculatum.

Tall-grass prairies and open woodlands. Michigan and Minnesota south to Nebraska, northeastern Texas and southern Illinois.

Dichantherium acuminatum (Sw.) Gould & Clark. *Ann. Missouri Bot. Gard.* 65: 1121. 1978.

Gould and Clark recognized eight varieties in this species encompassing all of the taxa treated in this paper. Four of the eight varieties I have treated above as distinct species (D. villosissimum for var. villosum, D. wrightianum for var. wrightianum, D. spretum for var. densiflorum, and D. longiligulatum for var. longiligulatum). I agree with their treatment of var.s lindheimeri and thurowii. I do not agree with their handling of the western U.S. hot-springs or geyser taxa which Spellenberg studied or with their handling of the hairy, non-robust component which comprises the most abundant and most variable part of the complex. Gould and Clark divided this latter group into var. implicatum (Scribn.) Gould & Clark and var. acuminatum, separating them entirely on the basis of spikelet length (1.2-1.5 mm vs. 1.6-2.5 mm), admitting that this separation was arbitrary. Shinnars and Pohl have both shown that there is a continuity in spikelet lengths in this complex with the mode of the curve for the distribution of specimens according to spikelet

length at about 1.6 mm. The two tables presented below show a tally of MIL, USWP, and WIS specimens by spikelet length. Table number one includes all specimens of varieties acuminatum and implicatum according to Gould and Clark's key (including specimens which I identify as D. commonsianum (Ashe) Freckm. var. euchlamydeum (Shinners) Freckm., D. leucothrix, D. meridionale, and D. acuminatum var.s sericeum and thermale). Table number two tallies the specimens of the three most common varieties of D. acuminatum as identified according to the keys presented in this paper.

Spikelet length in mm	Table No. 1. Specimens of <u>D. acuminatum</u> var.s <u>acuminatum</u> and <u>implicatum</u> sensu Gould and Clark.			Table No. 2. Specimens of three <u>D. acuminatum</u> var.s sensu Freckmann.		
	Wis. collections	Out-of-state	Total	<u>acum-inatum</u>	<u>fasci-ulatum</u>	<u>lindheim-eri</u>
1.2		2	2	1		
1.3	9	19	28	1	15	6
1.4	72	73	145		113	33
1.5	161	168	329	4	274	66
1.6	198	159	357	11	276	43
1.7	106	119	225	17	190	23
1.8	38	70	108	18	82	6
1.9	13	20	33	4	23	
2.0	10	5	15	2	9	
2.1	5	6	11		5	
2.2	17	11	28			
2.3	18	9	27			
2.4	23	12	35			
2.5	5	2	7			

It is evident from both tables that the separation of varieties entirely on the distinction of spikelets 1.6 mm or more vs. 1.5 mm or less is completely unsatisfactory. The type and to a lesser extent the distribution and density of hairs seem to provide a better set of characters. These traits are primarily under genetic control, although transplant studies indicate that stoutness is partially influenced by environmental factors and that hairs tend to break off or become more matted during the course of the growing season.

Key to the varieties of D. acuminatum:

1. Primary (vernal) culms usually less than 30 cm tall; mid-culm sheaths nearly as long as the internodes, their blades at least one-eighth as wide as long, generally more than 6 mm wide and less than 6 cm long..... var. sericeum
1. Primary (vernal) culms usually more than 30 cm tall; mid-culm sheaths about one-half as long as the internodes, their blades generally more than eight times as long as wide and more than 6 cm long.
  2. Sheaths and internodes of primary culms gray-villous with a dense, tangled to matted mixture of slender hairs 2-4 mm long, variously ascending, spreading, and retrorse, arising from small papillae or non-papillose, plus shorter hairs 0.2-1 mm long; winter rosette blades large, some exceeding 5 cm in length.
  3. Primary culms robust, generally more than 60 cm tall and 2 mm thick; panicle contracted, usually more than 8 cm long and less than one-half as wide..... var. thurowii
  3. Primary culms not exceptionally robust, rarely more than 60 cm tall or more than 1.3 mm thick; panicle broadly ovoid, less than 8 cm long and more than one half as wide.
    4. Primary panicles at fruiting stage exerted on peduncles less than 6 cm long; blades erect, those of late season lacking cilia on upper half..... var. thermale
    4. Primary panicles at fruiting stage generally exerted on peduncles more than 10 cm long; blades ascending to spreading, bearing cilia most of their length.....  
..... var. acuminatum
2. Sheaths and internodes of primary culms glabrous or papillose-pilose to hispid, with ascending straight hairs 1-3 mm long; winter rosette blades usually broadly ovate, spreading, 2-5 cm long.
  5. Peduncle and panicle axis pubescent to pilose; sheaths papillose-pilose to hispid, the hairs tending to break off, but leaving evident papillae..... var. fasciculatum
  5. Peduncle and panicle axis glabrous; sheaths, or at least middle portion of sheaths lacking hairs or papillae.....  
..... var. lindheimeri

Dichantherium acuminatum (Sw.) Gould & Clark var. acuminatum

Synonyms include P. lanuginosum Ell., P. auburne Ashe, and P. olivaceum Hitchc. & Chase.

Several names which Gould and Clark placed in synonymy here I assign to other taxa: P. thermale = var. thermale; P. tennesseense Ashe, P. huachucae Ashe, P. occidentale Scribn., P. subvillosum Ashe, P. pacificum Hitchc. & Chase, P. languidum Hitchc. & Chase, P. brodiei St. John, and P. lassenianum Schmolli = var.



fasciculatum; and P. ferventicola Schmoll = var. sericeum. P. benneri Fern. is discussed under D. villosissimum. P. shastense Scribn. & Merr. is a hybrid between D. acuminatum and D. oligosanthos (Spellenberg, 1970) and the same is probably true of P. scoparioides Ashe. I am not able to render a decision on the poorly known P. glutinoscabrum Fern., but I suggest that it is a hybrid between a member of the D. acuminatum complex and D. scoparium (Lam.) Gould - the latter contributing the genes for height and viscid sheaths.

This variety represents the densely hairy end of the spectrum which grades into var. fasciculatum and to var. lindheimeri at the glabrous end. Nevertheless the majority of specimens of this variety show a correlation among the traits given in the key, making the distinction between these three varieties more satisfactory than the acuminatum-implicatum distinction based on spikelet length.

Disturbed areas and open woodland, on thin, often sandy or clayey soils. Southeastern U. S., mostly on the Coastal Plain; West Indies; Mexico, Central America, and northern South America.

Dichantherium acuminatum (Swartz) Gould & Clark var. thermale (Bolander) Freckmann, comb. nov.

Basionym: Panicum thermale Bolander, Calif. Acad. Sci. Proc. 2: 181. 1862; Dichantherium lanuginosum (Ell.) Gould var. thermale (Bolander) Spellenberg. Madrono 23: 151. 1975.

On mineralized crust of warm, moist soil at The Geysers, Sonoma Co., California.

Dichantherium acuminatum (Swartz) Gould & Clark var. sericeum (Schmoll) Freckmann, comb. nov.

Basionym: Panicum ferventicola Schmoll var. sericeum Schmoll, Madrono 5: 92. 1939.

Synonyms: P. ferventicola Schmoll, P. ferventicola var. papillosum Schmoll, and D. lanuginosum (Ell.) Gould var. sericeum (Schmoll) Spellenberg.

Usually on warm or hot ground around geysers and hot springs. Rocky Mountains from Banff to Yellowstone National Park to Bighorn Co., Wyoming.

Spellenberg (1968 and 1975b) discussed both varieties in detail, noting that each variety retained distinguishing traits under greenhouse transplant conditions.

Dichantherium acuminatum (Swartz) Gould & Clark var. thurowii (Scribner & Smith) Gould & Clark. Ann. Missouri Bot. Gard. 65: 1125. 1978.

Dry, open woodlands. Georgia to east Texas.

Dichantherium acuminatum (Swartz) Gould & Clark var. fasciculatum (Torrey) Freckmann, comb. nov.

Basionym: Panicum dichotomum L. var. fasciculatum Torrey, Fl. North and Mid. U. S. 145. 1824.

Synonyms include P. implicatum Scribn., P. tennesseense Ashe, P. huachucae Ashe, P. occidentale Scribn., P. subvillosum Ashe, P. huachucae var. silvicola Hitchc. & Chase, P. pacificum Hitchc. & Chase, P. languidum Hitchc. & Chase, P. brodiei St. John, P. lassenianum Schmolli, D. lanuginosum (Ell.) Gould var. fasciculatum (Torr.) Spellm., and D. acuminatum var. implicatum (Scribn.) Gould & Clark.

This variety constitutes the most variable component of the complex. It intergrades with varieties acuminatum and lindheimeri and apparently hybridizes with D. oligosanthos, D. dichotomum (L.) Gould, D. boreale (Nash) Freckm., D. meridionale, D. columbianum (Scribn.) Freckm., D. sphaerocarpon (Ell.) Gould, and probably with several other species. Certain combinations of characters occur more frequently and have encouraged workers to accept some of the species listed above, including P. implicatum (numerous small spikelets, large multicomound panicles, and long erect hairs on upper blade surfaces); P. huachucae (larger spikelets, less compound panicles, short appressed hairs on blades); P. tennesseense (glabrous blades); and P. subvillosum (larger spikelets with relatively long first glumes, leaves and branches concentrated at base of plant). However, so many specimens show other combinations of traits that maintaining these as species or varieties requires annotating a high percentage of specimens as "atypical" or "intermediate."

Disturbed areas, open or cut-over woods, thickets, grasslands, sedge meadows, shores, etc., frequently on soils with upper horizon removed or scarred. Temperate North America, more discontinuous in the West and tending to be replaced by var. acuminatum in warm temperate and subtropical regions.

Dichantherium acuminatum (Swartz) Gould & Clark var. lindheimeri (Nash) Gould & Clark. Ann. Missouri Bot. Gard. 65: 1127. 1978.

Synonyms include P. lanuginosum var. septentrionale Fern. and D. lanuginosum var. lindheimeri (Nash) Freckm.

This variety represents the glabrous extreme of var. fasciculatum. Hybrids between D. acuminatum and either D. dichotomum or D. boreale are frequently identified as this variety; these hybrids usually have purplish spikelets nearly 2.0 mm long, wide, spreading blades, and a clear distinction between the short ring of ligule hairs and the scattered long hairs.

Same habitats as var. fasciculatum but with a greater preference for moist areas. Same range as var. fasciculatum.

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